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THE RELATIONSHIP OF THE OXYGEN CONSUMPTION TO THE CONTRACTION OF THE CAT PAPILLARY MUSCLE

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Most studies of the relationship between the oxygen consumption and the work of the heart have been performed *in vivo* or with isolated but intact heart preparations; and relatively few investigators have used isolated strips of cardiac muscle (Starling & Evans, 1914; Evans & Matsuoka, 1915; Gollwitzer-Meier, Kramer & Krüger, 1936; Lee, 1954). Since the influence of haemodynamic changes can be completely eliminated in studies with isolated muscle strips, the information obtained with such preparations is useful for an understanding of energy–work relationship in the cardiac muscle itself. Previously the author has reported on studies of this type, utilizing a manometric method which allowed the simultaneous measurement of oxygen consumption and of contraction of the papillary muscle from cat heart (Lee, 1953). Although this method was satisfactory for certain purposes, it had some disadvantages, the major one being its limited sensitivity to changes of oxygen concentration. Since in such investigations extremely small and thin muscles must be used to insure an adequate oxygen diffusion throughout the tissue, the sensitivity of the device for measuring oxygen concentration has to be extremely high. The present paper describes the experiments in which a method of adequate sensitivity based on a polarographic device for the measurement of the oxygen concentration in the medium was utilized to study the relationship of the oxygen consumption to the contraction of the cat papillary muscle under various experimental conditions. In addition, the newly designed apparatus for this work also permitted variation of tension on the muscle during the course of a single experiment. Special attention was focused upon the influence of tension and the frequency of contraction on the oxygen consumption and contractility of the papillary muscle.

METHODS

The principle of the polarographic device used by Carlson, Brink & Bronk (1950) for their studies on the oxygen consumption of nerve was applied to measuring the oxygen concentration of the medium. The system consisted of a muscle chamber, recording systems for electrode current and contraction, stimulating apparatus and a syringe driver device.

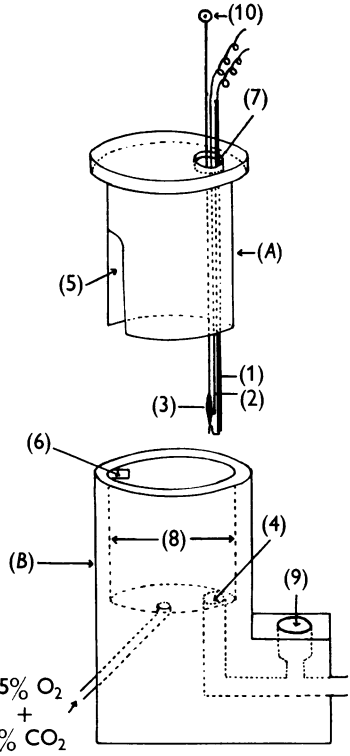

Fig. 1. Diagram of the muscle chamber. *A*, muscle holder; *B*, perfusion reservoir; 1 and 2, stimulating electrode; 3, muscle; 4, capillary channel, diameter 2·5 mm; 5, guide rail; 6, guide projection; 7, orifice for stimulating electrodes, diameter 6 mm; 8, fluid bath, diameter 3·9 cm; 9, orifice for oxygen electrode holder, diameter, 7 mm; 10, RCA transducer tube 5734.

The muscle chamber was made of lucite and consisted of a muscle holder and a perfusion-fluid reservoir. Figure 1 is a diagrammatic outline of the chamber. At the top of the muscle holder (*A*) was a 6 mm diameter opening through which stimulating electrodes and a thread from one end of muscle were passed. The stimulating electrodes (1 and 2) were made of platinum insulated with polyethylene tubing. The papillary muscle (3) was tied to one electrode of the muscle holder and was guided into a 2·5 mm diameter capillary channel (4) of the fluid reservoir (*B*), which opened at the bottom of the latter as shown in Fig. 1. A plastic plug containing an oxygen electrode was inserted into a 7 mm diameter opening (9) to the capillary channel distal to the muscle.

The arrangement of the entire system is shown in Fig. 2. The electrode-current-recording system consisted of a Northrup Speedomax galvanometer with chopper amplifier (*G*),

a 1·5 V battery (*BE*), a calomel half-cell (*D*) and an oxygen electrode (*E*) in circuit. The oxygen cathode was made of a platinum wire (0·005 in., 0·127 mm diam.) and a supporting glass rod (2 mm outside diam.). The platinum wire was sealed into a glass tube and then the sealed end of the glass tube was carefully ground on a plastic block to expose a clear round cross-section of the platinum wire. The tip of the electrode was covered with a polyethylene membrane tied with a fine silk thread. This electrode was inserted through the centre hole in the plastic electrode holder and fixed in the proper position with de Khotinsky cement.

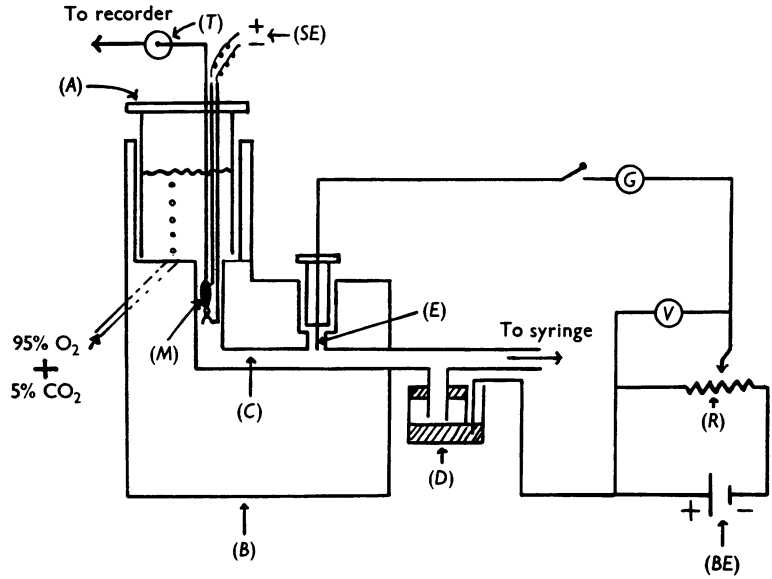

Fig. 2. Diagram of the entire recording system. *A*, muscle holder. *B*, perfusion fluid reservoir. *BE*, 1·5 V battery. *C*, capillary channel. *D*, calomel half cell. *E*, oxygen electrode. *G*, galvanometer. *M*, papillary muscle. *R*, rheostat. *SE*, stimulating electrodes. *T*, RCA transducer tube 5734. *V*, voltmeter.

After a muscle was placed in the capillary channel the thread from the muscle was connected to a spring which was in contact with an RCA transducer tube 5734 (T). Muscles were stimulated by a Grass Stimulator (Model S4) and the development of the isometric contractile tension of muscles was recorded on a Sanborn Twin Viso through the RCA tube. An extremely accurate constant-flow rate syringe driver (Baltimore Instrument Co.) which met the specifications required for the present study, pulled the perfusion fluid from the reservoir through the capillary channel (*C*) past the muscle, as indicated by the arrow, at a constant rate of 0·9966 ml./hr or 1·892 ml./hr. This rate of flow was selected so that the maximum extraction of oxygen by the muscle from the perfusing fluid would not exceed more than 25 % of total oxygen present in the solution, thus simulating the physiological condition of oxygen extraction. A gas mixture of O_2 95 + CO_2 5 % was continuously bubbled through the reservoir. The distance between the closer end of the muscle and the oxygen electrode was 1·2 cm. The distance between the tissue and the oxygen electrode, which is required for a uniform oxygen tension across the stream at the electrode in the solution, was calculated according to the formula given by Carlson *et al.* (1950) and found to be 0·37 cm under the present conditions. Therefore the distance between the muscle and electrode in this case was more than adequate to insure a homogeneous concentration of

oxygen across the stream at the position of the oxygen cathode. When the oxygen cathode was made several tenths of a volt negative with respect to the calomel half-cell, by adjusting the rheostat (*R*) in the presence of a battery (*BE*), oxygen molecules around the oxygen cathode were electrolytically reduced, the rate of reduction of oxygen being proportional to the concentrations of oxygen. The current flowing through the oxygen cathode was recorded on the galvanometer (*G*) and measured the oxygen concentrations in the solution at the electrode after it had been pulled past the muscle at a constant flow rate. In this method it is necessary to calibrate the individual electrode for different concentrations of oxygen before use. With all electrodes used in this work the electrode current measured by the galvanometer was linearly proportional to the oxygen concentration present in the solution. The theoretical principles basic to this polarographic method have been described previously (Connelly, Bronk & Brink, 1953).

All experiments were carried out at 37° C, in Krebs–Ringer solution with bicarbonate buffer (Umbright, Burris & Stauffer, 1957). To maintain this temperature the muscle chamber was placed in the constant-temperature box made of lucite. All Q_{O_2} values in this study were calculated on a wet weight basis. Since the perfusion fluid had to travel the distance between the muscle to the oxygen electrode, there was a time lag between the actual change of oxygen concentration at the muscle and its reflexion at the oxygen electrode. This time lag was found to be 7·5 min with the flow rate of 0·9966 ml./hr. In all the experiments a correction was made for this lag in order to obtain the actual temporal relationship between the oxygen consumption and the contraction of muscle. Muscles having diameters ranging from 0·3 to 0·6 mm were selected in order to insure the adequate oxygenation of the whole muscle, since it had been found that muscles having a diameter larger than 1 mm were inadequately oxygenated at the centre of the muscle (Lee, 1953).

RESULTS

Resting respiration of papillary muscle

The oxygen consumption of a muscle in the resting state without tension was studied in twenty-four experiments. The weight of the wet muscles ranged from 1·5 to 4·5 mg and the average Q_{O_2} on a wet-weight basis was found to be 1·16, with a standard error of 0·28. This Q_{O_2} of resting muscle without tension will be referred to as a 'basal resting Q_{O_2}'.

Effect of tension of resting muscle on the oxygen consumption

The application of tension to resting muscle was accompanied by an increase in Q_{O_2}. This increment of Q_{O_2} of resting muscles due to increase in resting tension will be referred to as a 'tension Q_{O_2}'. Figure 3 illustrates the relationship between the tension applied to resting muscle and the oxygen consumption of the muscle in a typical experiment. Over a range of muscle tension from 0 to 12 g/mm^2 of muscle, the Q_{O_2} increased progressively as the tension increased. A further increase in muscle tension beyond 12 g/mm^2, however, was accompanied by an insignificant change in the oxygen consumption. Table 1 summarizes the results obtained at three different tensions. The average maximal increase in the Q_{O_2} of resting muscle due to increased tension was 93 % ± 7·9 (S.E.) of the 'basal resting Q_{O_2}', and the average minimum tension required for this maximal increase in Q_{O_2} was 13 g/mm^2 ± 2·5 (S.E.).

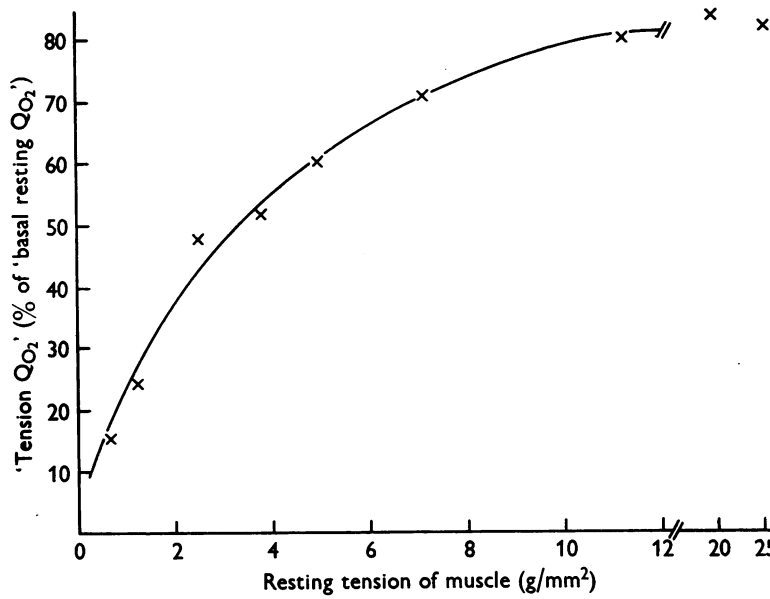

Fig. 3. The effect of resting tension on oxygen consumption of non-contracting muscle. Muscle diameter 0·37 mm; wet weight 2·8 mg.

TABLE 1. Effects of resting tension on oxygen consumption

No. of expts.	Tension (g/mm²)	Mean 'tension Q_{O_2}' (% of 'basal resting Q_{O_2}' ± S.E.)
7	2	32 ± 6·1
9	6	66 ± 8·3
7	12	89 ± 7·9

Changes in oxygen uptake by muscle during contraction

When the muscle was stimulated electrically at a constant frequency under a given tension, the rate of oxygen consumption increased to a new constant value. When the stimulation was terminated the rate of oxygen uptake gradually subsided to the previous resting level. A tracing of a typical record of the effect of a period of stimulation on electrode current is presented in Fig. 4. The decrease in current during the period of stimulation measured the increase in the amount of oxygen removed by the muscle from the passing medium. Since the flow rate and calibration constant were both unvarying, the change in the current was proportional to the change in the rate of extraction of oxygen from the solution. The difference in electrode current between the initial and final steady values measured the change in rate of oxygen consumption caused by the contraction of the muscle. This increment of Q_{O_2} due to contraction will be

referred to as 'activity Q_{O_2}'. As is seen in Fig. 4, during the isometric contraction of a papillary muscle initiated by electrical stimulation at a rate of 60/min, the increment of tension due to isometric contraction (contractile tension) reached a plateau in a few minutes where it remained relatively steady over many hours. Both the transition in the rate of oxygen consumption on going from the resting state to a state of rhythmic contraction, and the transition on returning to the resting rate, are described by exponential functions of time, except for the initial phase of each transition; but the time constant of the latter transition is longer than that of the former.

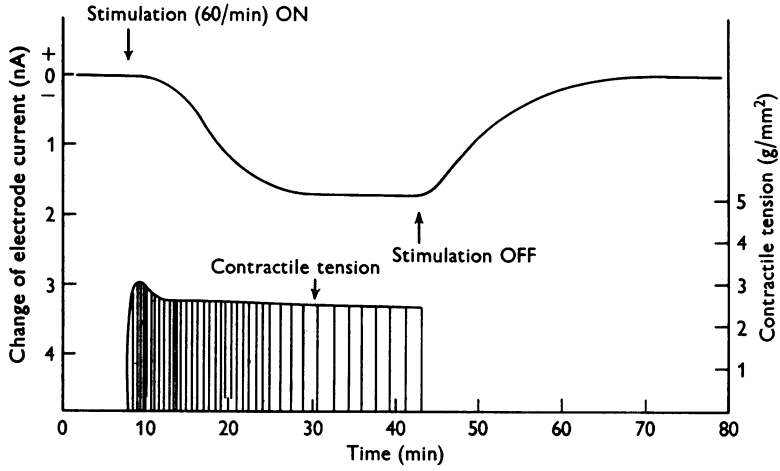

Fig. 4. The change in electrode current and contractile tension before, during and after electrical stimulation of the papillary muscle. Muscle diameter 0·32 mm; wet weight 3·8 mg; tension 2 g/mm².

Effect of the frequency of stimulation on the 'activity Q_{O_2}' and contractility

In these experiments the tension of the resting muscle was kept constant and the frequency of stimulation was varied over a range of 10–150/min. Both the increment in the oxygen consumption due to contraction ('activity Q_{O_2}') under a given resting tension, and the contractile tension developed, were dependent on the frequency of contraction. Results obtained in a typical experiment are shown in Fig. 5. It should be noted that at lower frequencies of stimulation there is a rise in 'activity Q_{O_2}' as the frequency of stimulation is increased. However, at a rate of 110/min or greater further increase in the rate of stimulation did not result in a significant increase in the oxygen consumption. Initially the increase in the frequency of contraction was accompanied by an increment in the contractile tension. However, a further increase in the rate of stimulation

above 70/min (in the expt. in Fig. 5), was accompanied by a reduction in the contractile tension. The mean values of contractile tension and 'activity Q_{O_2}' for different frequencies are given in Table 2.

The 'activity oxygen consumption per contraction' was calculated by dividing 'activity Q_{O_2}' by frequency of contraction per hour, and the

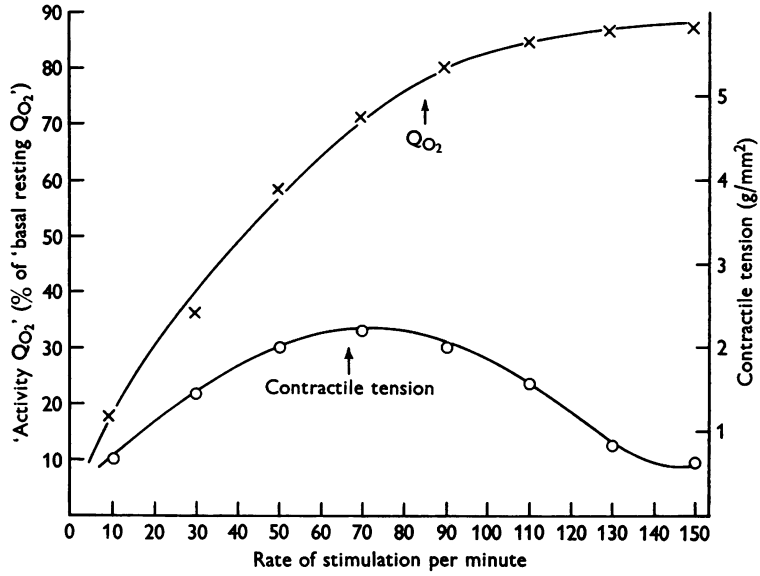

Fig. 5. The effect of frequency of stimulation on oxygen consumption and contractile tension developed by the muscle. Muscle diameter, 0·41 mm; tension, 4 g/mm²; wet weight, 4 mg.

TABLE 2. Effects of frequency of contraction on oxygen consumption and contractile tension

No. of expts.	Rate of contraction (per minute)	'Activity Q_{O_2}' (% of 'basal resting Q_{O_2}' ±S.E.)	Contractile tension (g/mm², ±S.E.)
6	30	39±8	1·3±0·16
5	70	73±11	2·8±0·32
5	110	91±16	1·5±0·28

Resting tension of muscle ranged between 3 and 6 g/mm².

values for different frequencies are given in Table 3. This table makes it clear that there is an inverse relationship between the frequency and the 'activity oxygen consumption per contraction'.

The ratio of isometric contractile tension : 'activity oxygen consumption per contraction', was calculated for each frequency of stimulation and was assumed (for reasons discussed later, p. 197) to represent an index of the mechanical efficiency of the muscle. A plot of this ratio against frequency

in a typical experiment is shown in Fig. 6. In this experiment efficiency rose to a maximum at around 90/min and then declined at higher frequencies.

TABLE 3. Activity oxygen consumption per contraction

Rate of contraction (per min)	10	30	60	90	120	150
Q_{O_2} per contraction ($\times 10^{-4}$ ±S.E.)	3·25±0·36	2·78±0·22	2·38±0·19	1·83±0·09	1·27±0·12	1·03±0·14

The oxygen consumption per contraction $= \frac{Q_{O_2} \text{ due to contraction}}{\text{rate of contraction per hour}}$; resting tension of muscle ranged between 4·1 and 6·6 g/mm².

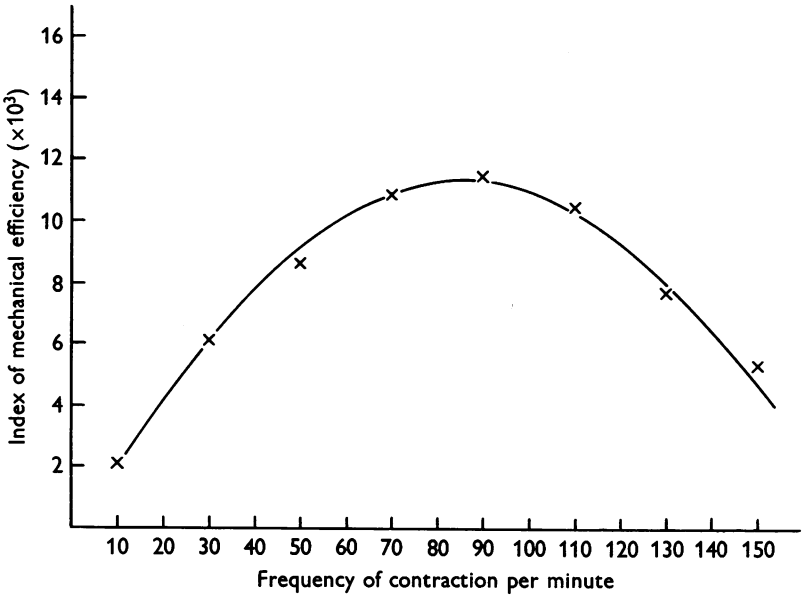

Fig. 6. The effect of frequency of contraction on the mechanical efficiency of the papillary muscle. Muscle diameter, 0·5 mm; wet weight, 7 mg; tension, 4 g/mm².

Effect of resting tension on the 'activity Q_{O_2}' and contractile tension of muscle being stimulated at a constant frequency

In muscles stimulated at a rate of 60/min, it was found that both the contractile tension and 'activity Q_{O_2}' varied with the resting tension. As is shown in Fig. 7, at low to moderate resting tension the 'activity Q_{O_2}' increased as the resting tension was increased. However, a further increase of the resting tension beyond approximately 12 g/mm², led to a slight decrease in the 'activity Q_{O_2}. An increase in the contractile tension also occurred as the resting tension of the muscle was increased up to

approximately 6 g/mm². However, a further increase in the resting tension (beyond 6 g/mm²) was accompanied by a considerable decline in the contractile tension. This decline in contractile tension beyond a certain resting tension is in accord with Starling's law (1915). A summary of the results concerning the effect of resting tension on the 'activity Q_{O_2}' and on the contractile tension is given in Table 4.

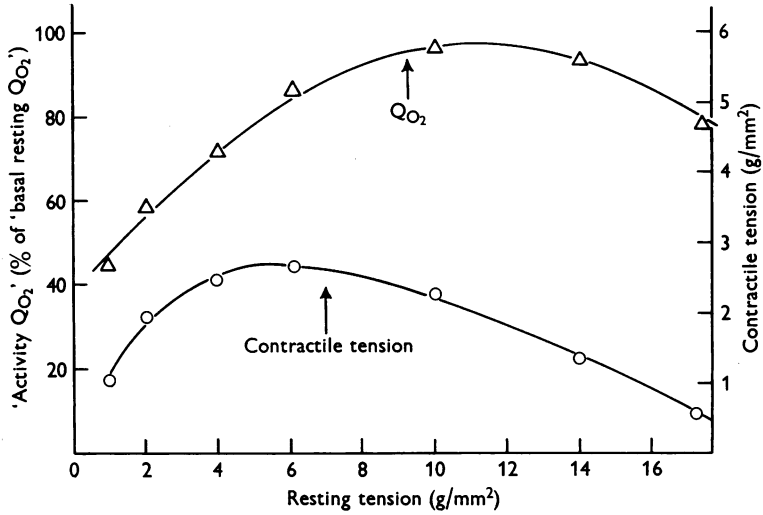

Fig. 7. The effect of resting tension on the activity respiration and tension developed by the muscle during contraction. Muscle diameter, 0·43 mm; wet weight, 3·2 mg. Stimulation frequency, 60/min.

TABLE 4. Effects of resting tension on oxygen consumption and contractile tension

No. of expts.	Resting tension (g/mm²)	'Activity Q_{O_2}' (% of 'basal resting respiration', ± S.E.)	Contractile tension (g/mm², ± S.E.)
6	1	39 ± 9	1·0 ± 0·21
5	4	66 ± 8·6	2·42 ± 0·35
6	10	99 ± 11·2	2·1 ± 0·33

The ratio, isometric contractile tension : 'activity oxygen consumption per contraction', at various resting tensions was calculated as described previously and taken as a hypothetical index representing the mechanical efficiency of these resting tensions. In Fig. 8 this index is plotted against the tension of the resting muscle. In the experiment illustrated, as well as in other similar experiments, efficiency rose sharply with resting tension, reached a maximum at about 3 g/mm² and then declined with further increase in tension.

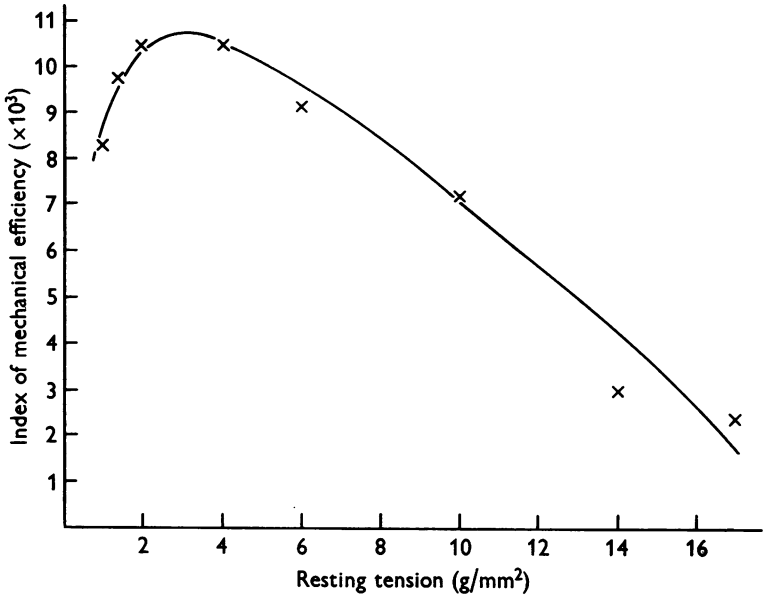

Fig. 8. The effect of resting tension on the mechanical efficiency of the papillary muscle. Muscle diameter, 0·35 mm; wet weight, 4·1 mg; stimulation frequency 60/min.

The relationship between resting tension, total oxygen consumption and length of muscles contracting at a constant rate

The contributions of the 'basal resting Q_{O_2}', the 'tension Q_{O_2}' and the 'activity Q_{O_2}' to the total Q_{O_2} in a single experiment were determined as follows. The muscle was first placed in the chamber without tension and the 'basal resting Q_{O_2}' was determined. The tension of the resting muscle was then brought to the desired level and the 'tension Q_{O_2}' was determined. Finally, the muscle at this tension was stimulated at a rate of 60/min, and the 'activity Q_{O_2}' was determined.

At a stimulation frequency of 60/min, the length and the total oxygen consumption of muscles were functions of the resting tension. The relationship between the Q_{O_2} and the length in a typical experiment is shown in Fig. 9. Initially, the total oxygen consumption increased progressively as the resting tension increased, reached a maximum at approximately 10 g/mm² of resting tension and then declined slightly at higher tensions. This slight decrease in the total Q_{O_2} at higher tensions was mainly due to the decrease in 'activity Q_{O_2}' at these tensions. On the other hand, the length of the muscle gradually increased as the tension was increased up to 16 g/mm², beyond which further increase did not change the length significantly. Thus, both the total oxygen consumption and muscle length

increased as the testing tension was increased up to 10 g/mm²; however, beyond this tension the former declined despite the continued increase of the latter. The proportions contributed by resting, tension and activity Q_{O_2} to the total Q_{O_2} of this muscle are also shown in this figure. The total oxygen consumption at three different testing tensions was analysed into various components, and the results are summarized in Table 5. It is seen that the proportions these components contribute to the total oxygen consumption vary with resting tensions.

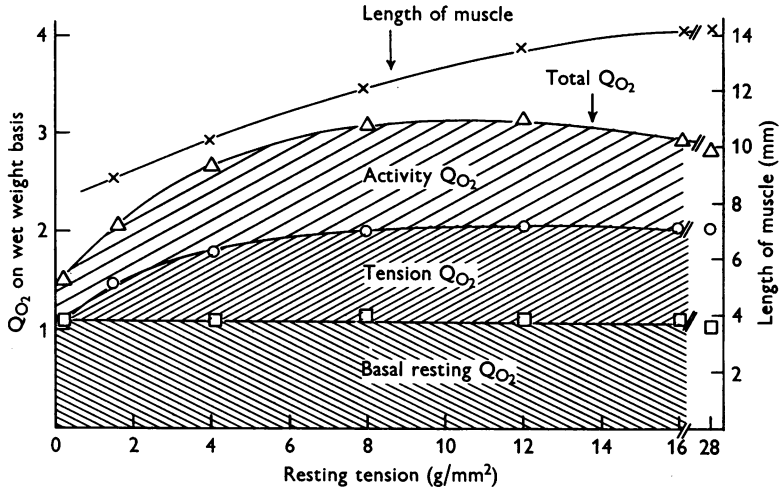

Fig. 9. The effect of resting tension on the length and oxygen consumption of the papillary muscle. Muscle diameter, 0·4 mm; wet weight 5 mg.

TABLE 5. Effects of resting tension on total oxygen consumption

No. of expts.	Resting tension (g/mm²)	Total Q_{O_2} ± S.E.	'Basal resting Q_{O_2}'* ± S.E.	'Tension Q_{O_2}'* ± S.E.	'Activity Q_{O_2}'* ± S.E.
5	1·2	2·2 ± 0·21	54 ± 7·6	16 ± 4·2	28 ± 5·5
6	6	2·7 ± 0·31	38 ± 7·1	29 ± 6·2	34 ± 6·2
9	12	3·35 ± 0·29	34 ± 8·8	32 ± 7·7	33 ± 8·8

* Expressed as % of total Q_{O_2}.

DISCUSSION

The technique described in this paper for the measurement of oxygen tension has been found to be highly satisfactory for the quantitative study of the oxygen uptake of isolated papillary muscles. As discussed in a previous paper (Lee, 1953) the thickness of the muscles used was well within the limit necessary for the adequate diffusion of oxygen throughout. In the resting state without tension, the Q_{O_2} of muscles, on a wet weight basis, was found to be 1·16. An increase in the tension applied to resting

muscle was accompanied by a gradual increase in the Q_{O_2}. The maximum increase in the Q_{O_2} due to an increase in the tension on the muscle was reached when the tension approximated 13 g/mm^2. The average maximum Q_{O_2} due to tension was about 90 % of the 'basal resting Q_{O_2}'. This would indicate the importance of the influence of resting tension on the oxygen uptake of heart muscle.

Contraction, initiated by electrical stimulation, was found to increase the Q_{O_2} of the muscle as shown in Fig. 4. In this figure both the transition from the steady resting respiration to the steady active respiration following the initiation of contraction and the reverse transition following the cessation of contraction can be expressed by exponential functions of time. This temporal relationship characterizing the increase and decrease of respiration following the initiation and cessation of the contraction may describe the characteristics of the sequence of processes linking contraction with aerobic metabolism.

When muscle was contracting isometrically under a constant resting tension, both 'activity Q_{O_2}' and the contractile tension were found to vary with the frequency of contraction. Over the range of lower frequencies of contraction, both 'activity Q_{O_2}' and contractile tension were increased as the rate of stimulation was increased. The maximal contractile tension under constant resting tension was reached when the frequency of contraction was in the range of 60–90/min. When the frequency was further increased beyond this range, however, the 'activity Q_{O_2}' increased on one hand and the contractile tension decreased on the other. The maximal 'activity Q_{O_2}' under a constant resting tension was obtained when the muscle contracted at approximately 110/min, and reached about 90 % of the 'basal resting Q_{O_2}'. When the 'activity Q_{O_2}' is divided by the frequency of contraction per hour and this ratio is assumed to be the 'activity oxygen consumption per contraction', it is seen in Table 3 that an inverse relationship holds between the frequency of contraction and the 'activity oxygen consumption per contraction'.

The relationship between the 'activity Q_{O_2}' and contractile tension under a constant resting tension is expressed in terms of a hypothetical mechanical efficiency for various frequencies in Fig. 6. As was described above, the index of mechanical efficiency was calculated by the ratio, contractile tension : 'activity oxygen consumption per contraction'. Although the assumption that the oxygen consumption is a constant index of the energy production of the heart may be inaccurate *in vivo*, owing to factors such as changing respiratory quotient, this assumption is considered to be reasonably valid in this study, since glucose was the only substrate available in the medium and hearts of warm-blooded animals contract on an oxygen debt only for a brief period, if at all (Evans, 1939; Gollwitzer-

Meier, 1939). Thus the above ratio may reasonably be assumed to be an indicator of the mechanical efficiency. If so, Fig. 6 suggests that, when a papillary muscle is contracting under a constant tension, the highest mechanical efficiency is observed at stimulation frequencies of 60–100/min, and the efficiency decreases at both higher and lower frequencies.

When the muscle is contracting isometrically at a constant frequency (60/min), both the 'activity Q_{O_2}' and the contractile tension vary with the resting tension (Fig. 7). Over a range of lower tensions both the 'activity Q_{O_2}' and the contractile tension increase as the resting tension is increased. The maximum contractile tension is obtained when the muscle is contracting under a resting tension of 4–8 g/mm^2. When the resting tension is increased further, the 'activity Q_{O_2}' increases on one hand and the contractile tension decreases on the other. The maximum 'activity Q_{O_2}' is observed when the muscle is contracting under a resting tension of 10–14 g/mm^2. Thus it is seen that, when a muscle is contracting at a constant rate, the maximal oxygen consumption is obtained at a greater resting tension than that at which the maximal contractile tension is obtained. Previously Evans & Hill (1914) found the same relationship between the heat production and the contractile tension during isometric contraction of *frog* skeletal muscle at different resting tensions. If the oxygen consumption is considered to be a reasonable index of heat production in the present experiment, these results would indicate that the relationship between the contractile tension, heat production and the initial tension found in frog skeletal muscle also applies to a mammalian cardiac muscle.

When the hypothetical index for the mechanical efficiency is calculated as described previously for different resting tensions, it is seen (Fig. 8) that the mechanical efficiency rises sharply over the range 0–3 g/mm^2. The change in mechanical efficiency of heart muscle under varying diastolic volume has been the subject of many studies (Starling & Visscher, 1927; Moe & Visscher, 1939; Katz, Jochim, Lindner & Landowne, 1941; Wise, Meyer, Katz, Lendrum & Jochim, 1946). Starling & Visscher (1927) found that as the heart goes into failure while the diastolic volume increases, there is a decrease in the mechanical efficiency. The validity of their conclusion was questioned because of inherent difficulties involved with whole-heart preparation in the measurement of the true mechanical efficiency (Katz, 1955). The major difficulty was that the work done by the heart could not be correlated with the oxygen uptake due to activity only and total oxygen uptake had to be used in their calculation. In the present study the index of mechanical efficiency was calculated by using the oxygen consumption due to activity only, and the interference by other factors was completely eliminated. Under these experimental con-

ditions, the results shown in Fig. 8 indicate that the mechanical efficiency of the heart muscle starts to decline when the initial resting tension increases beyond 4 g/mm^2. Since the length of muscle continues to increase as the resting tension is increased beyond 4 g/mm^2 (Fig. 9), the present conclusions are in accord with the finding of Starling & Visscher (1927) that an increase in the diastolic volume beyond certain limits is accompanied by a decrease in the mechanical efficiency. It is interesting to consider the mechanical efficiency of the cat papillary muscle under varying resting tensions and frequencies of contraction. When the frequency is the only variant the muscle has the highest mechanical efficiency over the range of 60–100/min. When the resting tension is the only variant the muscle has the highest mechanical efficiency over the range of 2–4 g/mm^2 of the resting tension. Thus it appears that a muscle contracting at a rate of 60–90/min under a resting tension of 2–4 g/mm^2 has the highest mechanical efficiency.

When muscles contract at a rate of 60 beats/min, analysis of the total oxygen consumption (Fig. 9 and Table 5) shows that the 'activity Q_{O_2}' and 'tension Q_{O_2}' occupy a greater proportion of the total oxygen consumption at higher resting tensions and the 'basal resting Q_{O_2}' occupies a greater proportion at lower resting tensions. The maximal total oxygen uptake of muscle contracting at a rate of 60/min is observed when muscles contract under a resting tension of 12 g/mm^2 or more. Under these conditions the 'tension Q_{O_2}' and the 'activity Q_{O_2}' are approximately 80 and 89 % of 'basal resting Q_{O_2}'. It is interesting to note that at the maximal total oxygen uptake of muscle, the activity, the tension and the resting state each accounts for approximately one third of the total oxygen uptake. The total Q_{O_2} at this time would be approximately 270 % of 'basal resting Q_{O_2}' corresponding to 3·14. On the other hand, under conditions giving the maximal efficiency, namely, with a resting tension of 2–4 g/mm^2 and a frequency stimulation of 60 min, the 'tension Q_{O_2}' and 'activity Q_{O_2}' would amount to approximately 50 and 70 % of the 'basal resting Q_{O_2}', respectively.

SUMMARY

1. A system is described whereby, by using polarographic principles for the determination of oxygen concentration and an RCA transducer for recording contractions, the simultaneous measurement of oxygen consumption and of contraction of the electrically stimulated cat papillary muscle is achieved. With this system the influence of tension and frequency of stimulation on the oxygen consumption and mechanical efficiency of the papillary muscle has been investigated.

2. An increase in the resting tension produced an increase in the oxygen consumption of resting muscle. The maximal increase in the Q_{O_2} of the resting muscle was obtained when the resting tension was 12 g/mm^2 or greater.

3. Electrical stimulation of the muscle produced an increase in the Q_{O_2}. This 'activity Q_{O_2}' increased as the frequency of stimulation increased and reached a maximum at a frequency of 110/min or greater.

4. The papillary muscle contracting under a constant tension has its greatest mechanical efficiency at a stimulation frequency of approximately 90/min. On the other hand, with a constant frequency of stimulation the greatest mechanical efficiency was attained under a resting tension of about 3 g/mm^2.

5. The extent of contribution of each of the following—the 'resting Q_{O_2}', 'tension Q_{O_2}' and 'activity Q_{O_2}'—to the total Q_{O_2} of the contracting muscle was found to be influenced by the initial resting tension of the muscle.

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